Plant water relations and photosynthesis during and after drought in a Chihuahan desert arroyo

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Abstract

In order to understand the physiology and ecology of perennial shrub species occupying the banks of ephemeral streams we studied the plant water relations and gas-exchange characteristics of six perennial shrub species growing along an ephemeral stream (arroyo) in the northern Chihuahuan Desert. Two of the species are restricted to riparian habitats (*Brickellia laciniata* and *Chilopsis linearis*), three are classified as semi-riparian (*Fallugia paradoxa*, *Prosopis glandulosa*, and *Rhus microphylla*) and one is considered to be non-riparian (*Flourensia cernua*). Differences in gas-exchange patterns and water relations emerged among these six species, yet differences among obligate, semi-riparian, and non-riparian classes of species were evident, but not universal. *Chilopsis* and *Brickellia* did not develop the low plant water potentials that characterized some semi-riparian (*Rhus*) and non-riparian species (*Flourensia*) during periods of drought. Rates of photosynthesis and transpiration were highest in *Prosopis* throughout the study, and were relatively constant in *Chilopsis* during and after drought. Whether water became available as channel flow or direct rainfall appeared to play a role in the physiology of these arroyo shrubs.
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1. Introduction

The warm deserts of the south-western United States are water-limited ecosystems (Thames and Evans, 1981) in which the deleterious effects of temporally sparse and spatially heterogeneous rainfall are compounded by high rates of evaporation and surface runoff. Much of the surface runoff flows into drainage channels called arroyos that transport water downslope into ephemeral playas or perennial water catchments. The volume of water transported in an arroyo during and after a storm is a function of the characteristics of the storm, soil type, desert vegetation, and position of the arroyo in the landscape (Ludwig and Whitford, 1981; Wondzell et al., 1987).

Water flow in arroyos is infrequent but intense, usually leaving the arroyo channel bed devoid of vegetation. The arroyo banks, however, support a shrub flora substantially different from the adjacent desert proper. Species composition is partially different, density of perennial plants is lower, and plant size and canopy cover are greater along arroyos (Balding and Cunningham, 1974; Ehleringer and Cooper, 1988). Beyond such general attributes, however, little is known about the physiology and ecology of perennial shrub species occupying the banks of arroyos.

The shrub flora of arroyo margins consists of species that are exclusively restricted to riparian habitats, and those that are not (Dick-Peddie, 1993). During a study designed in part to compare ecophysiological attributes of these classes of arroyo shrub species (Killingbeck and Whitford, 2001), an extended period without a channel-filling event (drought) ended. A flash flood coursed through the arroyo in which we were working for the first time in 620 days. We utilized this fortuitous occurrence as a natural experiment that allowed us to examine the physiological responses of arroyo plants to release from drought stress.

In this paper we report on the gas-exchange physiology and plant water relations of six perennial shrub species growing along the banks of an arroyo in the northern Chihuahuan Desert. Each of the six species was classified as either obligate riparian (occurring only along the banks of arroyos), semi-riparian (occurring in riparian areas and in surrounding desert areas) or non-riparian (normally not occurring in riparian areas). Non-riparian species probably occur in riparian areas due to arroyo channel encroachment into former desert areas. Our initial objective was to determine whether these sympatric arroyo shrubs differed in their abilities to fix carbon and acquire water. The specific null hypotheses tested were that there were no significant differences in photosynthetic gas-exchange and leaf water potential characteristics among arroyo species in general, and between obligate riparian, semi-riparian, and non-riparian species in particular. The serendipitous cessation of drought provided a means by which we could also test the null hypothesis that there were no significant differences in the abilities of these six species to recover from drought stress.

2. Materials and methods

2.1. Study site and plant material

The community studied was located along the banks of an arroyo on the Chihuahuan Desert Rangeland Research Center approximately 40 km NNE of Las Cruces, New Mexico, USA. The arroyo studied (Arroyo J-1) is a major drainage of a watershed of the Doña Ana Mountains. The remainder of the watershed is desert grassland dominated by black grama (*Bouteloua eriopoda* (Torr.) Torr.) and desert shrubland dominated by creosotebush (*Larrea tridentata* (Sesse & Moc. Ex DC.) Coville). The vegetation of the 335-m segment of arroyo we sampled included the six species of shrubs selected for study; two obligate riparian species (*Brickellia laciniata* Gray, cutleaf brickellbush and *Chilopsis linearis* (Cav.) Sweet, desert willow), three semi-riparian species (*Fallugia paradoxa* (D. Don) Endl., apache plume, *Prosopis glandulosa* Torr., mesquite, and *Rhus microphylla* Engelm. Ex Gray, littleleaf sumac), and one non-riparian species (*Flourensia cernua* DC., tarbush).

Rhus are winter deciduous, multi-branched, multi-stemmed shrubs with small, rounded leaves that grow to approximately 2 m along arroyo margins. *Chilopsis* are winter deciduous small trees or shrubs of between 3 and 5 m height with linear-lanceolate leaves that grows in arroyo beds or margins. *Fallugia* are dense, 1–2 m tall multi-branched shrubs with leaves that are more or less evergreen. These shrubs grow in dense linear clumps along the margins of arroyos. *Flourensia* are highly resinous, multi-branched, 1 m tall, winter deciduous shrubs that are primarily an upland species which occurs along arroyo margins in some areas. *Brickellia* are 1–2 m tall, winter deciduous, dense multi-stem–multi-branched shrubs that grow in arroyo beds and along arroyo margins. *Prosopis* are 3–4 m tall, winter deciduous, small trees or shrubs with straight spines and pinnately compound leaves that grow along arroyo margins. This shrub composition was the most diverse of any segment along an arroyo in the watershed studied (personal observation). In this watershed *Yucca elata* and *Atriplex canescens* was observed to occur infrequently along the banks. Only one other shrub species, *Larrea* commonly occurred along the arroyo banks along the lower reaches of the arroyo, usually in the absence of the other shrub species.

We selected four individuals of each species, two on each bank of the 4–15 m wide arroyo segment, with at least 5 m between shrubs of the same species, sufficient distance to ensure that they were functionally independent. At the upslope and downslope ends of the arroyo segment we positioned two lines of chalk dust. Chalk lines are relatively undisturbed by wind or rainfall, but surface flow along the arroyo channel washes the chalk away. These lines were first established in January 1993 as part of another study (Atchley et al., 1999). This segment of arroyo had flowed ten times between January 1993 and October 14, 1994, but did not flow again until June 26, 1996.

Precipitation and air temperature data for the area were obtained from the Jornada Long Term Ecological Research project (Jornada LTER) weather station located approximately 2 km north of the arroyo site. The long-term mean for rainfall

in the region is 250 mm, 64% of which occurs during convectional storms from July through September (Jornada LTER data). Summer maximum temperatures frequently reach 40°C and winter minima below 0°C occur regularly from November to February (Jornada LTER data).

2.2. Plant water status

Before dawn on each measurement day we excised leaves or terminal stem segments with leaves from each experimental plant and measured plant xylem water potential using the techniques described by Scholander et al. (1965) with a 3000 series Plant Water Status Console (Soilmoisture Equipment Corp., Santa Barbara, CA). Plant xylem water potentials were measured on 4 days in 1996: June 25 and 29, July 11, and August 14.

2.3. Gas-exchange

We selected and tagged two leaves (*Prosopis*, *Flourensia* and *Rhus*) or stem segments with leaves (*Brickellia*, *Chilopsis*, and *Fallugia*) on each plant with colored pipe cleaners. The tags allowed us to find and identify the leaves or stem segments used for repeated gas-exchange measurements during a measurement day. We used an LI 6200 Portable Photosynthesis Measurement System (LI-Cor, Inc., Lincoln, NE) with a 0.25 liter leaf cuvette to measure gas-exchange characteristics of the plants. During a measurement day we made every effort to keep the LI6200 near ambient air temperature by keeping the system under shade except during gas-exchange measurements when the cuvette was exposed to direct sunlight. Net photosynthesis (P_{net}) transpiration rate (E), stomatal conductance (g_s), leaf-internal CO_2 concentration (C_i) and atmospheric (ambient) CO_2 concentration (C_a) and associated factors such as leaf and air temperatures, photosynthetically active photon flux density (PPFD) and the partial pressure of water vapor in air were all measured with the LI6200. Other factors such as leaf-to-air vapor pressure deficit were calculated from these measurements using standard equations. Plant gas-exchange was measured on the same days as was pre-dawn xylem water potential. We took two measurements on each of the 24 plants five times during a day. Only three sets of measurements were taken on June 29, 1996 because of rain. At the end of a measurement day, leaves (or stems with leaves) used for gas-exchange measurements were harvested, stored in plastic bags, and taken to the laboratory where leaf area was measured with a LI 3000 Leaf Area Meter (LI-Cor, Inc., Lincoln, NE). Data were then entered into the LI 6200 computer to derive gas-exchange rates on the basis of single-surface leaf area.

2.4. Statistical analyses

Statistical analyses were performed with SigmaStat software (SigmaStat Statistical Software, 1995). Two-way analysis of variance (ANOVA) was used to determine whether the physiological variables measured were a function of sampling date and

species. When significant differences were confirmed, Tukey's test was used to differentiate among means. Differences were considered statistically significant when probability levels were <0.05.

3. Results

3.1. Climate and flow events

The daily maximum and minimum temperatures and precipitation for 1996 as recorded at the Jornada LTER weather station are shown in Fig. 1. On June 25, 1996, the first day we took measurements, all species except *Prosopis* appeared to be severely water stressed. *Brickellia*, *Chilopsis*, *Fallugia Flourensia*, and *Rhus* had few leaves, and the leaves that were present were very small. This arroyo segment had not experienced a flow event since October 14, 1994 and there had been only 23 mm of low-intensity rainfall since October 1995. Before dawn on June 26 a high intensity, high volume rain event caused the arroyo to flow across its entire width at our experimental site. Continued evening thunderstorms over the next 4 days caused large flow events again on June 28 and 29. More rain occurred in early August, before our final measurements but the arroyo did not flow during this time.

3.2. Plant water relations

During the first intense drought, plant water potentials (ψ_L) were highest in the riparian species *Chilopsis* followed by *Brickellia* and the three semi-riparian species (*Fallugia*, *Prosopis*, *Rhus*) and lowest in the non-riparian *Flourensia* (Fig. 2). The ψ_L of all species increased following the rain and channel-filling events of June 25
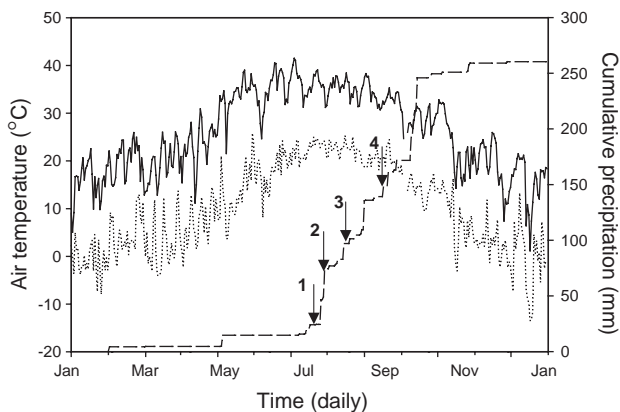

Fig. 1. Daily maximum (—) and minimum (⋯⋯) air temperatures and cumulative precipitation (- - -) measured at the Jornada LTER weather station, approximately 2 km north of the experimental site during 1996. Plant water potentials and gas-exchange were measured on the 4 days indicated with arrows (1 = June 25; 2 = June 29; 3 = July 11; and 4 = August 14).
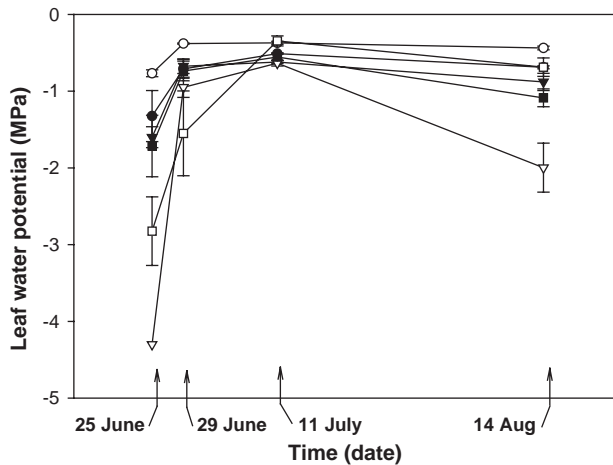
Fig. 2. Mean pre-dawn plant water potentials for the six experimental species, *Brickellia* (●), *Chilopsis* (○), *Fallugia* (▼), *Flourensia* (▽), *Prosopis* (■), and *Rhus* (□) measured on 4 days during 1996. Error bars indicate standard errors.

through June 28, 1996, and only *Rhus* had a ψ_L significantly lower than *Chilopsis* and *Fallugia* on June 29 (Fig. 2). The greatest relative increase in ψ_L during this time of rehydration occurred in *Flourensia* (78%) and the smallest increase was in *Rhus* (45%). The absolute change in ψ_L between June 25 and 29 was smallest in *Chilopsis* (0.39 MPa), but its percent change was 50%. Although the arroyo did not flow between June 30 and July 11, ψ_L increased in all species. *Rhus* had the greatest increase (78%) and *Chilopsis* the least (3%). There were no significant differences in ψ_L among species on July 11 (Fig. 2). By August 14, ψ_L in *Flourensia* was significantly lower than in all other species and had decreased by 158% since July 11 (Fig. 2).

3.3. Gas-exchange

Five sets of measurements were taken on June 25, July 11, and August 14, but only three sets of measurements were possible on June 29 due to rain. Therefore, the diurnal patterns of gas-exchange for this day are not shown. Rates of P_{net}, g_s, E, and the ratio C_i/C_a for the six plant species during the period of extended drought, on June 25, are shown in Fig. 3. P_{net} and g_s of all six species were highest early in the day and decreased thereafter. Five of the six species had very similar patterns of gas-exchange and only *Prosopis* had mean P_{net} greater than $10 \, \mu mol \, m^{-2} \, s^{-1}$. Mean E was greatest during the early afternoon, and the daily mean C_i was $240 \pm 25 \, \mu mol$ with C_i/C_a being greatest during the early morning and late afternoon. Among the shrub species C_i values were comparable except for *Flourensia* which was significantly higher than *Brickellia* or *Chilopsis* (Table 1). Measurements taken soon after the first drought-breaking flow event (June 29) showed no substantial changes in gas-exchange rates or patterns. However, we found substantial increases in
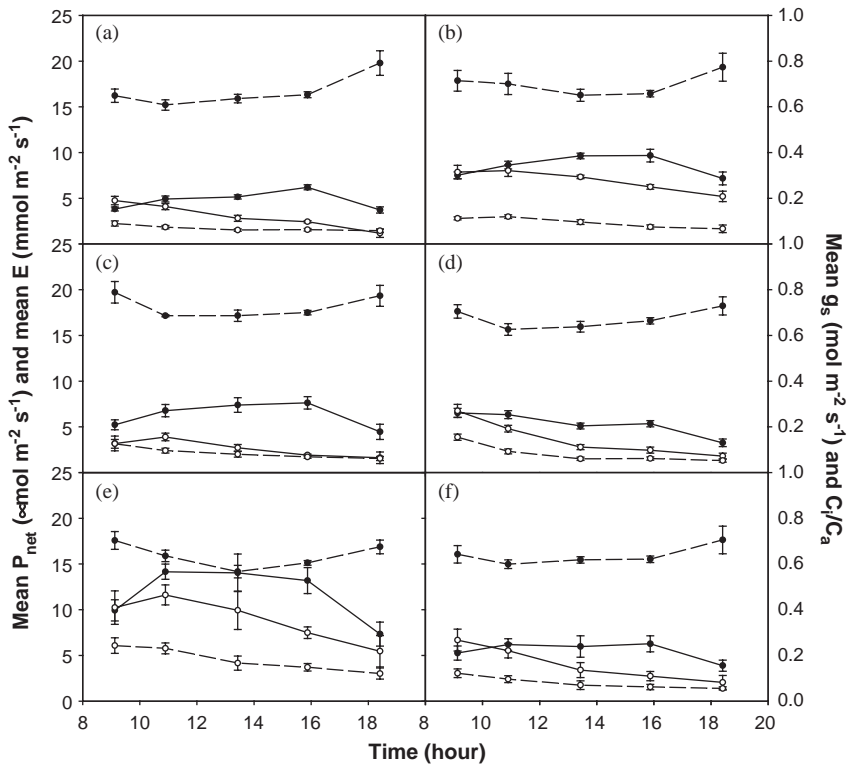
Fig. 3. Diurnal patterns of mean net photosynthetic rates (—○—), transpiration rates (—●—), the ratio of leaf-internal CO_2 concentration to ambient CO_2 concentration (--○--), and stomatal conductance rates (--●--) for *Brickellia* (a), *Chilopsis* (b), *Fallugia* (c), *Flourensia* (d), *Prosopis* (e), and *Rhus* (g) measured on June 25 during a long-term drought. Error bars indicate standard errors and $n = 8$.

gas-exchange rates in all species on July 11, approximately 2 weeks after the first arroyo flow-event (Fig. 4). The only exception to this increase was P_{net} in *Chilopsis* which remained at levels similar to those found during drought (June 25). At this time the mean C_i of all species except *Prosopis* and *Flourensia* was higher than during the drought (Table 1). While there were increases in overall gas-exchange rates we found that the diurnal patterns were very similar to those found during the period of extended drought when P_{net} and g_s were greatest during the early part of the day and decreased thereafter, E was greatest during early afternoon, and C_i/C_a was greatest during early morning and late afternoon measurements. Approximately one month later, on August 14, following some rainfall (Fig. 1) but no arroyo channel flow events, the gas-exchange rates of all species had returned to levels similar to those found on June 25 (Fig. 5), indicating the presence of another drought. A notable difference was the significantly lower mean C_i concentration of all species measured on this day (Table 1), although diurnal patterns of C_i/C_a were similar to those found on 25 June and 11 July.

Table 1
Mean leaf internal CO_2 concentrations ($n = 12$) for each shrub species on the four sampling dates

Shrub	Mean leaf-internal CO_2 concentration (ppm)			
	June 25	June 29	July 11	August 14
Brickellia	254.7±12.2abA	276.6±7.4abAB	285.5±7.6aB	190.5±4.0aC
Chilopsis	227.1±3.8aA	264.0±9.1aB	284.2±7.2aB	204.3±7.2aC
Fallugia	248.6±7.2abA	294.2±8.8bdeB	297.0±3.4aB	223.2±6.8bC
Prosopis	242.7±19.2abA	232.9±7.5aeA	249.8±7.0cA	191.4±7.5aB
Rhus	237.9±8.2abA	272.6±9.3dB	263.1±7.2bB	188.9±4.5aC
Flourensia	268.4±15.1bA	313.6±11.3cB	243.2±6.7bcA	200.0±5.1aC

Significant differences in means ($p < 0.05$) based on Tukey's test are indicated using different lower case letters for comparisons among species within a date (columns) and different upper case letters are used for comparisons among dates for each species (rows).
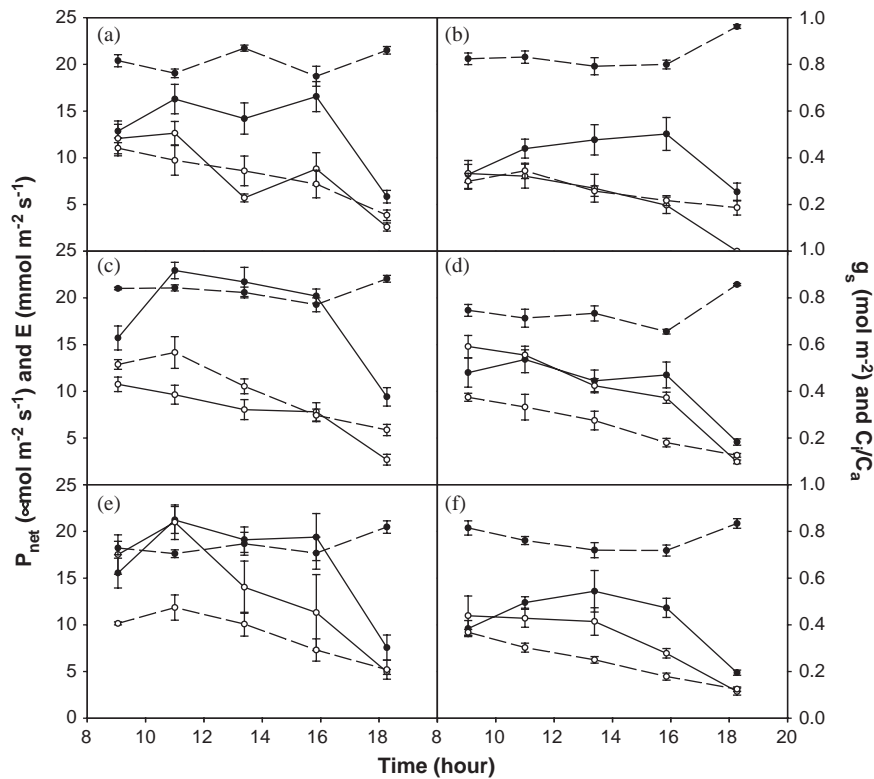

Fig. 4. Diurnal patterns of mean net photosynthetic rates (—○—), transpiration rates (—●—), the ratio of leaf-internal CO_2 concentration to ambient CO_2 concentration (- -○- -), and stomatal conductance rates (- -●- -) for *Brickellia* (a), *Chilopsis* (b), *Fallugia* (c), *Flourensia* (d), *Prosopis* (e), and *Rhus* (g) measured on July 11 two weeks after drought was alleviated. Error bars indicate standard errors and $n = 8$.
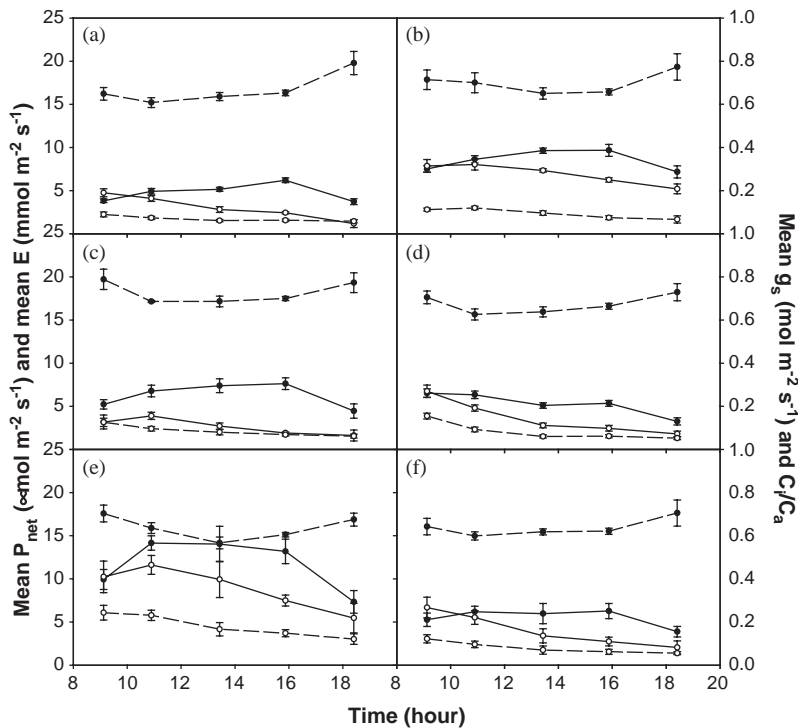
Fig. 5. Diurnal patterns of mean net photosynthetic rates (—○—), transpiration rates (—●—), the ratio of leaf-internal CO_2 concentration to ambient CO_2 concentration (- -○- -), and stomatal conductance rates (- -●- -) for *Brickellia* (a), *Chilopsis* (b), *Fallugia* (c), *Flourensia* (d), *Prosopis* (e), and *Rhus* (g) measured on August 14 during a second, less intensive drought. Error bars indicate standard errors and $n = 8$.

In order to statistically compare gas-exchange measured on the different days, we calculated an integrated photosynthetic rate (P_i; area under curve in mmol m^{-2}) and an integrated stomatal conductance (g_i; area under curve in mol m^{-2}) for the period of 4 h which encompassed the first three measurement sets only (see Figs. 3–5) in order to also accommodate measurements from June 29. The apparent similarity in rates of P_{net} and g_s observed on June 25 and August 14 was confirmed when P_i and g_i were compared for all six species (Table 2). There were no significant differences in P_i or g_i ($p < 0.05$; Tukey's test) for any species on these 2 days. Comparison of measurements taken during the intervening days however showed that P_i had increased significantly in all species except *Chilopsis* by July 11. In the case of stomatal conductance, g_i had increased significantly in all species by July 11 (Table 2). Of the six species studied, only *Rhus* had an immediate g_i response to alleviation of drought while both *Prosopis* and *Rhus* had an immediate P_i response (June 25 versus June 29; Table 2).

While there were differences in the diurnal patterns and in the magnitude of PPFD measured on different days, PPFD was always higher than 1250 μmol m^{-2} s^{-1}, which

Table 2
Mean integrated net photosynthetic rates, stomatal conductances, and their standard errors ($n = 6-8$) for each shrub species on the four sampling dates

Shrub	June 25	June 29	July 11	August 14
Integrated net photosynthetic rate (mmol m^{-2})				
Brickellia	74.1 $\pm$ 10.7aAE	120.1 $\pm$ 6.6aAC	165.5 $\pm$ 18.2abBC	60.0 $\pm$ 6.1aDE
Chilopsis	92.1 $\pm$ 5.5aA	116.8 $\pm$ 23.3aA	120.6 $\pm$ 11.9aA	73.6 $\pm$ 7.3aA
Fallugia	52.1 $\pm$ 8.9aA	84.6 $\pm$ 5.6aA	146.8 $\pm$ 8.4abB	53.6 $\pm$ 3.2aA
Prosopis	171.7 $\pm$ 42.9aA	271.3 $\pm$ 24.2cB	282.8 $\pm$ 15.7cB	163.4 $\pm$ 14.3bA
Rhus	55.4 $\pm$ 9.2aA	118.1 $\pm$ 6.9aBC	168.8 $\pm$ 19.0abB	81.0 $\pm$ 13.4aAC
Flourensia	79.7 $\pm$ 14.3aA	53.0 $\pm$ 15.8bA	199.6 $\pm$ 10.7bB	69.4 $\pm$ 3.5aA
Integrated stomatal conductance (mol m^{-2})				
Brickellia	1489 $\pm$ 117aA	2772 $\pm$ 342aA	6472 $\pm$ 852aB	1256 $\pm$ 148aA
Chilopsis	1672 $\pm$ 219aA	2678 $\pm$ 345aA	5617 $\pm$ 578aB	1963 $\pm$ 168bA
Fallugia	1066 $\pm$ 162aA	2534 $\pm$ 108aA	9324 $\pm$ 1075bB	1667 $\pm$ 181abA
Prosopis	3129 $\pm$ 641aA	4867 $\pm$ 330bA	7381 $\pm$ 765abB	3827 $\pm$ 236bA
Rhus	1072 $\pm$ 239aA	2918 $\pm$ 137aB	5199 $\pm$ 355aC	1715 $\pm$ 247abA
Flourensia	1757 $\pm$ 170aA	2839 $\pm$ 346aA	5503 $\pm$ 941aB	1738 $\pm$ 176abA

Significant differences in means ($p < 0.05$) based on Tukey's test are indicated using different lower case letters for comparisons among species within a date (columns) and different upper case letters are used for comparisons among dates for each species (rows).

is the nominal saturation point for photosynthesis in many desert plants (e.g. Franco et al., 1994).

4. Discussion

Clear differences in gas-exchange patterns and water relations emerged among the six species of shrubs we studied in the Chihuahuan Desert arroyo. Significant interspecific differences were evident for all physiological parameters on all but one sampling date. The single exception was the convergence of leaf water potentials on July 11. Among obligate riparian, semi-riparian and non-riparian classes of species, class-specific differences in physiological parameters were evident, but not universal. For example, leaf water potential in the non-riparian *Flourensia* was markedly different from that in the two obligate arroyo species *Chilopsis* and *Brickellia*, yet integrated photosynthesis and stomatal conductances were similar among these three species on most sampling dates.

Plants inhabiting arroyos may either respond quickly to cycles of water availability or they may be adapted to withstand these rapid fluctuations and maintain relatively constant photosynthetic rates and water potentials. Our data suggest that *Brickellia*, *Fallugia*, *Flourensia*, *Prosopis* and *Rhus* follow the former strategy. *Chilopsis* appears to follow the latter because the integrated photosynthetic rate of this species did not change significantly when drought was initially alleviated,

or during the second drought. The photosynthetic rates of the obligate riparian *Brickellia*, the three semi-riparian species, and the non-riparian *Flourensia* continued to increase beyond the period immediately following drought alleviation, and reached maximum rates on July 11.

The semi-riparian *Prosopis* usually had significantly higher rates of photosynthesis, stomatal conductance, and transpiration under both drought and "wet" conditions than did any of the other species. The obligate riparian *Chilopsis* had significantly higher water potentials during drought. *Chilopsis* and *Brickellia* did not develop the low plant water potentials that characterized some semi-riparian (*Rhus*) and non-riparian species (*Flourensia*) during periods of drought. Of the two obligate arroyo species, only *Chilopsis* is known to have a tap-root which is characteristic of phreatophytic species (Nilsen et al., 1984). The other potentially pheratophytic species, *Prosopis*, developed lower pre-dawn plant water potentials than did *Chilopsis*. Two non-phreatophytic semi-riparian species (*Flourensia* and *Rhus*) developed very low water potentials during drought and they, like *Brickellia*, *Chilopsis*, and *Fallugia*, also had few leaves and therefore probably only minimal whole-plant transpiration.

Arroyo channel-filling events usually occur during the summer in the northern Chihuahuan Desert, but they are rare. Much of the water entering an arroyo from a flow event is usually rapidly lost through lateral (downstream) and vertical (to deep soil) transmission (Wallace and Renard, 1967; Ludwig and Whitford, 1981; Lane, 1990). Plants growing along arroyo banks appear to be relatively unaffected by rainfall in the absence of channel-flow events. Between July 11 and August 14 there was substantial rainfall, but the arroyo did not flow. During this period, plant water potential decreased in *Flourensia*, stomatal conductance decreased in every species, and photosynthesis decreased in every species except *Chilopsis*. This suggests that for plants inhabiting arroyos, rainfall in the absence of arroyo flow may not be sufficient to provide sustained relief from drought.

Even though four of the six species maintained high to moderately high plant water potentials during drought, and environmental factors such as light intensity and air temperatures were in ranges that are normally not limiting, their integrated photosynthetic rates (mol CO_2 fixed/m^2 leaf area) were reduced during drought. This suggests that drought may affect photosynthesis through pathways other than those mediated directly through plant water potentials. It is possible that even though some species maintained relatively high water potentials during drought, overall accumulation of water and mineral resources was low. Therefore, insufficient resources available for investment in the photosynthetic apparatus, both structural and chemical, could conceivably have led to the low photosynthetic rates measured. Alternatively, the opposing demands of translocation and transpiration for limited water supplies may cause photosynthate to accumate in source leaves which, through negative feedback mechanisms, depresses photosynthesis (sensu Zolkevich et al., 1958). The few, small leaves present on the experimental plants during the initial drought support the former possibility, as do the C_i concentrations maintained in these leaves during the first drought.

The size of the stomatal aperture, as expressed by g_s, is a compromise between water loss and CO_2 intake (Farquhar et al., 1980; Wolfe, 1994; Leuning, 1995) and plants tend to regulate C_i such that for a given water vapor pressure deficit there is a constant C_i/C_a (Mott, 1990; Goudriaan and Unsworth, 1990). Under steady-state conditions C_i/C_a for C3 plants is approximately 0.67 (Goudriaan and Unsworth, 1990; Kimball et al., 1995), and the mean C_i/C_a of 0.64 exhibited during the first drought falls within this range.

However, our data also support the second possibility. During the second period of drought when plant water potentials were relatively high and leaf development had been completed, photosynthetic rates and g_s values of all species were again reduced to levels similar to those found during the first drought, but C_i values were significantly lower for all species. Given non-limiting light, temperature, and plant moisture conditions, and the similarity of these conditions between dates, the negative feedback hypothesis becomes a viable option. Elucidation of the relative contributions of these mechanisms will require further study involving experimental manipulation of plant environmental conditions including resource availability.

We conclude that while obligate, semi-riparian, and non-arroyo shrubs are different in their responses to drought and drought alleviation in some physiological characteristics, they are similar in others. Both obligate riparian species (*Brickellia* and *Chilopsis*) had characteristics such as high plant water potential in common, but gas-exchange in both species was often similar to that in the semi-riparian species. Overall, maximum photosynthetic rates of obligate arroyo species were lower than those of semi-riparian species, but obligate riparian species continued to have relatively high rates of photosynthesis and higher plant water potentials during drought. Finally, whether water becomes available as channel flow or direct rainfall appears to play a significant role in the physiology of arroyo shrubs. Therefore, the source of water as well as the amount and temporal distribution of water received likely act as a suite of selection pressures that influence the evolution of these arid land plant species.

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